

The natural diet of a polyphagous predator, *Latrodectus hesperus* (Araneae: Theridiidae), over one year

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Abstract. The natural diets of many terrestrial predators such as spiders have yet to be investigated. In this study, I analyzed the diet of a web-building spider, *Latrodectus hesperus* Chamberlin & Ivie (1935), over one year in a natural habitat of coastal British Columbia, Canada. This is the first study to document the natural diet of *L. hesperus* over several months. I identified and measured 1599 prey items collected from *L. hesperus* webs and web sites between January and December. Spiders fed on ground-active prey from eight different orders of arthropods. Coleoptera and Hymenoptera were the predominant prey of *L. hesperus* in this habitat, combinely accounting for > 85% of the total prey catches and biomass. The other prey orders included, in order of abundance, Isopoda, Araneae, Dermaptera, Orthoptera, Lepidoptera and Diptera. Spiders captured prey mostly between May and October, when females oviposit, juveniles grow, and prey are most active. These results show that *L. hesperus* is a polyphagous predator that feeds primarily on prey from two orders of insects.

Keywords: Feeding regime, foraging, predator-prey interactions, prey, spiders

An animal's diet breadth typically falls along a generalist-specialist continuum. One extreme is represented by generalist foragers that feed on a variety of organisms from different taxonomic groups; the opposite end consists of specialists that feed exclusively on a single type of organism or taxon, even when others are available to them. Most animals fall somewhere in between the two depending on the environment they live in and their foraging strategies (Futuyma & Moreno 1988).

Much research on animal diets has focused on terrestrial arthropods, and has documented the evolution of diverse patterns of resource use involving herbivory, predation and parasitism (Nentwig 1987; Jaenike 1990; Bernays & Minkenberg 1997). Spiders are important terrestrial predators that sit at the top of many invertebrate food webs and show varied feeding habits. They are for the most part polyphagous and prey upon a variety of invertebrate taxa across a broad range of habitats (Nentwig 1987; Riechert & Harp 1987). Yet, a few species specialize on prey, such as ant-eating zodariid spiders, araneophagic mimetid spiders, and moth-eating araneid spiders (Jackson & Whitehouse 1986; Stowe 1986; Pekár 2004).

A balanced diet composed of different prey types may be adaptive for spiders. Indeed, polyphagy provides access to a variety of nutrients not available from a single prey source, which may maximize growth rates and juvenile survival (Uetz et al. 1992; Toft & Wise 1999). However, a mixed diet may be constrained by the habitat-dependent availability of certain prey types. Under such constraints, spiders can maximize diet quality by selectively feeding on particular subsets of prey in the environment that may be abundant or highly nutritious (Riechert & Harp 1987; Futuyma & Moreno 1988).

Two empirical methods have commonly been used to study the feeding habits of spiders; both have provided ample evidence of the polyphagous nature of many spider species. The first one involves feeding experiments with different

assortments of prey. The results of such experiments have shown that some spiders feed indiscriminately on different prey types, while others show preferences for certain prey types based on particular morphological or behavioural attributes of the prey (e.g., Nentwig 1986; Toft & Wise 1999; Pekár 2004). The second method is used to characterize the actual range of prey consumed by a particular species in its natural habitat based on field surveys and observations (e.g., Robinson & Robinson 1970; Hódar & Sánchez-Piñero 2002; Guseinov 2006). Collectively, these field studies have shown that a spider's diet breadth may depend on its foraging strategy and the type of habitat it lives in. Given the great diversity of spiders, more studies in natural settings are needed to determine what a species *does* eat in relation to what it *can* eat.

The aim of this study is to characterize the diet of a locally abundant web-building spider, *Latrodectus hesperus* (Chamberlin & Ivie 1935) (Araneae: Theridiidae), over one year in a natural habitat of southwestern Canada. I collected and identified all prey items of *L. hesperus* spiders each month and analyzed their diet based on prey composition and numbers, prey size, prey biomass and prey-capture rate.

METHODS

Study area.—This study was conducted in a coastal sand dune habitat of southern Vancouver Island, British Columbia, Canada (48°34'N, 123°22'W, elev. 2–3 m), in an area located above the high-tide line and ~ 90 m from the shore. The study site was a ca. 600-m² area of open sandy habitat with interspersed clusters of driftwood logs, bordered by densely-spaced trees and shrubs (see Salomon et al. 2010 for details). The weather at this site is cool and wet from October–March and both warmer and drier between April–September.

Study species.—*Latrodectus hesperus* is a web-building spider that is native to western North America and found from Mexico to southwestern Canada (Kaston 1970). At the study site, *L. hesperus* is the dominant web-building spider. Furthermore, individuals are facultatively group living, i.e., they occur either solitarily or in small groups depending on habitat conditions and time of year (Salomon et al. 2010).

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Spiders live exclusively under driftwood logs found throughout the open sandy habitat and build three-dimensional cobwebs on the underside of the logs. Their webs are often quite extensive and have a central tangle region from which sticky 'gumfooted' silk lines designed to capture prey extend vertically to the ground.

General setup and prey-sampling method.—Thirty rectangular wooden sheds were placed in and around a large cluster of driftwood logs at the study site in early January 2003 as part of a 3-yr study of group living in *L. hesperus* (see Salomon et al. 2010). These sheds provided new habitat in which wandering *L. hesperus* spiders could establish themselves. The sheds were built with two 150 × 14 cm cedar boards that were orthogonally nailed together, and their dimensions corresponded to those of an average-sized driftwood log occupied by *L. hesperus*. *Latrodectus hesperus* spiders readily settled under the sheds and their populations persisted over several years (Salomon et al. 2010). This semi-natural setup was ideal for studying the diet of *L. hesperus*, as it provided uniform habitat space in which it was possible to reliably sample prey.

The current study was conducted from January–December 2005. By the time it was initiated, *L. hesperus* spiders were well established under the sheds and occupied 80–100% of the sheds year-round.

I counted the total number of *L. hesperus* spiders under each shed on a monthly basis in 2005 and collected their prey and identified them. In late December 2004, I cleared all prey remains from *L. hesperus* webs and the sandy substrate under the sheds. Starting in late January 2005 and continuing on a monthly basis until December, I collected all prey items that had been captured by spiders in the preceding month. This was done by carefully picking prey off the webs (unless spiders were still feeding on them) and collecting discarded prey from the substrate under the sheds. This protocol represents a very effective method of collecting prey of *L. hesperus*, yielding most, if not all, prey items. Two other web-building species co-occurred with *L. hesperus* under the sheds at low densities: *Tegenaria agrestis* (Walckenaer 1802) and *T. duellica* (Simon 1875) (Araneae: Agelenidae). Unlike *L. hesperus*, *Tegenaria* spiders usually macerate and compact their prey during consumption, rendering most remains unrecognizable as prey (extensive laboratory feedings with *T. agrestis* and *T. duellica* have shown that individuals practically always macerate and compact prey from various taxa; S. Vibert, unpublished data). I only collected prey items that were still whole or broken into recognizable pieces. It is thus very likely that most, if not all, of the collected prey were those of *L. hesperus* spiders because the integrity of their prey is preserved after consumption. I identified all prey items to order level under a stereo microscope and used various taxonomic keys as references.

Prey-capture metrics.—I quantified the number and proportion of prey from different arthropod orders that spiders captured each month, and determined prey composition as the diversity of prey orders captured. The degree of variation in prey composition was quantified using Levins' standardized index of diet breadth, $B_A = ((1/\sum p_i^2) - 1)/(n - 1)$, where p_i is the proportion of prey items from prey type i , and n is the total number of prey types (Hurlbert 1978; Krebs 1999). This index ranges from 0 to 1, with values close to 0 indicating that a predator consumes few prey types in high proportion, and

values close to 1 indicating that all prey are consumed in equal proportion. Note that this index does not account for differences in prey type availability in the habitat, which was not measured and thus cannot be controlled for in the analyses. I calculated monthly B_A values as well as an overall value for the whole study period. I also computed the inverse Simpson's index of diversity, $1/D = 1/\sum p_i^2$, which ranges from 1 to the total number of prey types, with higher values representing a greater diet breadth (Krebs 1999).

Prey size and biomass.—For all except Araneae (spider) prey, I measured the total body length of each prey item with digital callipers (to the nearest 0.01 mm) and used these data to calculate dry mass based on taxonomic order-specific regression equations available from the literature (see Appendix 1). Araneae prey were not always intact (e.g. some had deformed abdomens), so I measured the combined length of the tibia and patella of their first pair of legs (a reliable index of size in spiders; Jakob et al. 1996) instead of their total body length. The dry mass of Araneae prey was then calculated using regression equations developed for each of the three types of Araneae prey collected under the sheds: *Tegenaria* spp. (*T. agrestis* and *T. duellica*), *Latrodectus hesperus*, and Lycosidae. Only two Araneae specimens did not belong to these categories (1 salticid and 1 antrodiaetid spider; see Results); for these I used the regression equation developed for Lycosidae, which was judged to be sufficiently accurate for the purpose of this study.

To calculate dry mass from body size in *Tegenaria* spp. and *L. hesperus* prey, I developed two regression equations: a first one relating body size to wet mass and a second one relating wet mass to dry mass (Appendix 1). For the first equation, I measured the tibia-patella length of leg pair I (in mm; precision: 0.01 mm) and wet mass (precision: 0.1 mg) of 86 *L. hesperus* and 28 *Tegenaria* spp. (15 *T. agrestis* and 13 *T. duellica*) field-collected adult females, regressed both variables, and determined the fit of the regression using a General Linear Model (GLM). For the second equation, I weighed 32 *L. hesperus* and 16 *Tegenaria* spp. (8 *T. agrestis* and 8 *T. duellica*) field-collected adult females, killed them by freezing, dried them in an oven at 60 °C for 96 h, and re-weighed them once fully dry. From these wet mass data I calculated dry mass using a regression equation. To derive dry mass from body size in Lycosidae prey, I developed a single regression equation based on data from four species of lycosid spiders ($n = 32$; 8 specimens each of *Alopecosa kochi* (Keyserling 1877), *Arctosa perita* (Latreille 1799), *Pardosa* spp., and *Trochosa terricola* (Thorell 1856)) collected in pitfall traps around the study site from March–June 2003 as part of a separate study (M. Salomon & R.G. Bennett, unpublished data). I measured the tibia-patellar length of the first pair of legs of each spider, dried them using the protocol described above and weighed them when fully dry.

I used a General Linear Mixed Model (GLMM) to test for variation over time in average prey length per shed (log-transformed) based on data from all except Araneae prey, with month as a within-subject factor and shed identity as a subject factor.

RESULTS

Diet breadth.—The overall diet breadth of *L. hesperus* at the study site was 0.18 (standardized Levins' index, B_A), indicating

Table 1.—Prey of *Latrodectus hesperus* spiders in coastal British Columbia, Canada, between January–December 2005.

Prey taxon	Total number	% Total number	Total biomass (dry g)	% Total biomass	Body length (mm) (mean \pm SD (range))
Insects					
Coleoptera	974	60.91	2953.94	87.81	8.35 \pm 2.28 (4.66–24.19)
Hymenoptera	422	26.39	335.35	9.97	10.02 \pm 4.39 (4.97–21.70)
Dermaptera	32	2.00	2.32	0.07	10.36 \pm 1.60 (6.14–13.20)
Orthoptera	25	1.56	21.73	0.65	17.66 \pm 4.29 (10.34–25.71)
Lepidoptera	15	0.94	11.50	0.34	17.18 \pm 3.61 (13.64–28.26)
Diptera	5	0.31	0.83	0.03	10.76 \pm 0.91 (9.42–11.74)
Malacostraca					
Isopoda	69	4.32	18.95	0.56	9.06 \pm 1.30 (6.01–11.44)
Arachnids					
Araneae	57	3.57	19.54	0.58	—
TOTAL	1599	100.00	3364.16	100.00	—

that spiders preyed upon a few arthropod orders in high proportion and many orders in small amounts. Monthly B_A values ranged from 0.04 (in March) to 0.23 (in July) with a median of 0.16 from January–December. Overall diet breadth expressed as the inverse Simpson's index ($1/D$) was 2.25, and ranged from 1.25 (in March) to 2.62 (in July) with a median of 2.10. This means that *L. hesperus* fed predominantly on 2 prey orders.

Prey composition, size and biomass.—Between January and December, I collected and identified 1599 prey of *L. hesperus*. The diet of *L. hesperus* was composed of prey from 8 different orders of arthropods present in variable quantities (Table 1; Fig. 1a,b). Spiders fed primarily on beetles (order Coleoptera) that varied widely in body length, and these represented > 60% of all prey catches and > 80% of the total prey biomass (Table 1). The main types of Coleoptera prey were, in order of abundance: tenebrionid, curculionid and carabid beetles.

The second most abundant prey order was Hymenoptera, which included ants (Formicidae; 52.4% of Hymenoptera prey), sand wasps (*Bembix* sp. (Sphecidae); 26.1%), paper wasps (*Polistes* sp. (Vespidae); 10.4%), bumble bees (*Bombus* sp. (Apidae); 5.9%), ichneumonid wasps (Ichneumonidae; 4.0%), honey bees (*Apis* sp. (Apidae); 0.7%), and other sphecids wasps (Sphecidae; 0.5%). The smallest hymenopteran prey were ants and the largest were paper wasps (Table 1); the overall prey-size distribution of hymenopterans was bimodal with many large (wasps and bees; median length: 14.1 mm) and many small prey (mostly ants; median length: 6.0 mm).

The remaining orders of arthropod prey each represented < 5% of the total prey catch and < 1% of the total prey biomass (Table 1). These included, in order of abundance as prey, Isopoda, Araneae, Dermaptera, Orthoptera, Lepidoptera and Diptera. Spiders that were preyed upon included wolf spiders (Lycosidae, 77.2% of Araneae prey; primarily *Alopecosa kochi*, *Arctosa perita*, *Pardosa* spp. and *Trochosa terricola*), *T. agrestis* and *T. duellica* adults and juveniles (12.3%), *L. hesperus* adults, subadults and juveniles (7.0%), 1 male *Habronattus americanus* (Keyserling 1885) (Salticidae) and 1 female *Antrodiaetus pacificus* (Simon 1884) (Antrodiaetidae). Lycosid prey were 0.4–0.9 \times the average size of adult female *L. hesperus* (mean \pm SD tibia-patellar length of field-collected females: 6.46 \pm 0.33 mm, n = 86), whereas *Tegenaria* prey were 0.8–1.7 \times the average size of adult female *L. hesperus*.

Salticid and antrodiaetid prey were 0.3 and 0.9 \times the average size of adult female *L. hesperus*, respectively.

Overall, the distribution of prey lengths (i.e. all except Araneae) varied over time in accordance with the availability of different types of prey (GLMM: $F_{11,213.9} = 2.93$, $P = 0.001$; Fig. 1c). There was no clear seasonal pattern in prey-length distributions. Median prey length was highest in October (9.7 mm) and lowest in November (6.9 mm). The large majority of prey (90%) were 6–14 mm in length, i.e. 0.5–1.3 \times the average body length of adult female *L. hesperus* (females are generally 10.5–13 mm in length; Kaston 1970).

Timing of prey capture.—*Latrodectus hesperus* spiders captured prey year-round (Fig 1a), but most prey (78.9%) were captured from May–October when females produce egg sacs and emerging juveniles grow and mature (Fig. 1d; see also Salomon et al. 2010). Most prey orders showed temporal variation in the catch (Fig. 2). Coleoptera varied in abundance over time in the prey catch but were the dominant prey each month. Hymenoptera were common prey only from May–September, which corresponds to their season of peak activity at the study site (pers. obs.; Figs. 1a, 2). Sand wasps and bumble bees were captured during an even shorter time window, i.e. June–August. Other prey orders such as Isopoda and Orthoptera showed a peak in abundance between July–October (Fig. 2). *Latrodectus hesperus* fed upon con- and heterospecific spiders at a relatively constant rate, with a peak of predation on lycosids in April (Fig. 2).

DISCUSSION

The results of this study show that the diet of the web-building spider *L. hesperus* in coastal British Columbia, Canada, is characteristic of a polyphagous predator. *Latrodectus hesperus* spiders fed on eight different orders of ground-active arthropods, captured mostly from May to October, which is the period of oviposition and peak juvenile growth, when population densities are highest (Salomon et al. 2010). However, spiders were mostly insectivorous with two insect orders (Coleoptera and Hymenoptera) as their primary sources of prey. Of the two, Coleoptera made up the large majority of prey catches and especially prey biomass.

The diet breadth of *L. hesperus* is consistent with that of other web-building spiders (reviewed in Nentwig 1987 and Nyffeler 1999). Most web-building spiders are broadly

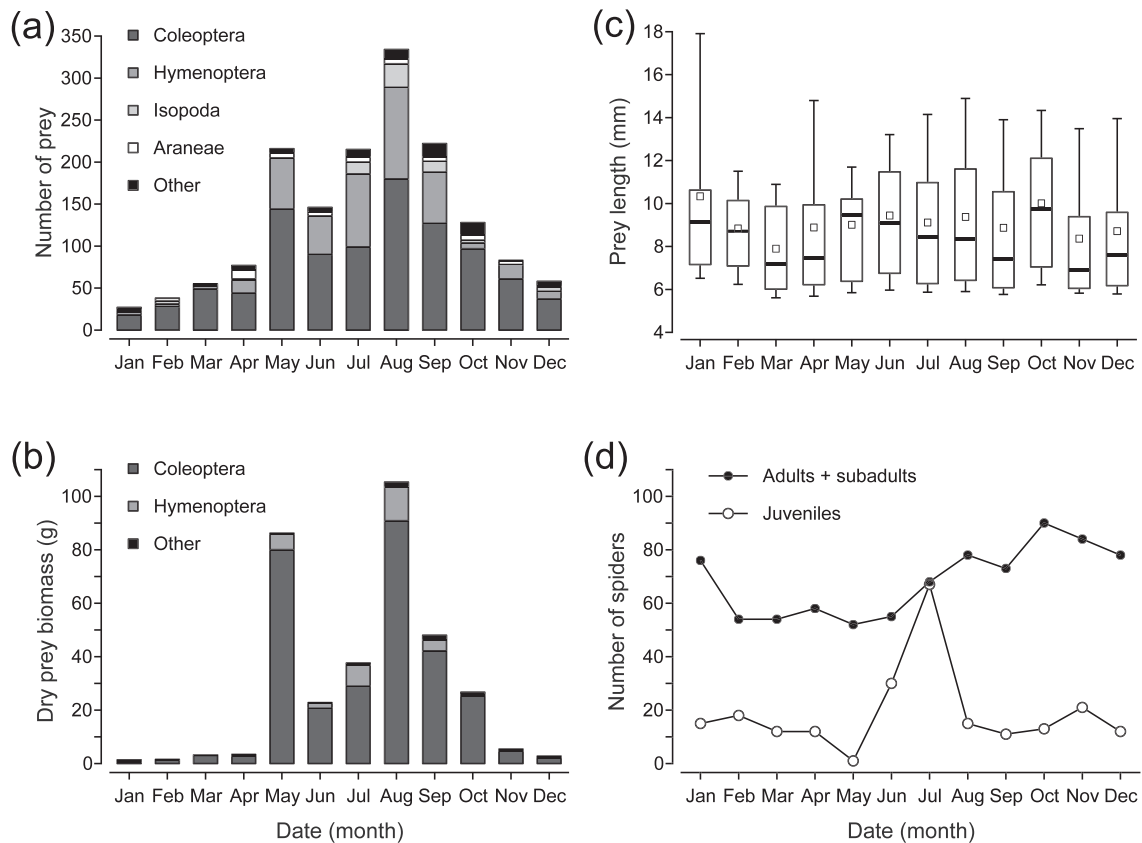


Figure 1.—Prey captured by *Latrodectus hesperus* spiders on a monthly basis in 2005: (a) number of prey; (b) prey biomass (dry); (c) prey length distributions. (d) Number of *L. hesperus* spiders from different age classes present under the sheds. In (a) and (b), prey are grouped according to their taxonomic order with the 4 most abundant orders shown separately and the remainder (Dermaptera, Orthoptera, Lepidoptera and Diptera) grouped into a single category, 'Other'. In (b), only the 2 most abundant orders are shown separately and the remainder is grouped into 'Other'. In (c), box plots show the median (thick lines), mean (open squares), 25th and 75th percentiles (bottom and top of boxes), and 10th and 90th percentiles (cap of lower and upper whiskers); Data for Araneae prey are omitted because they are not based on body length.

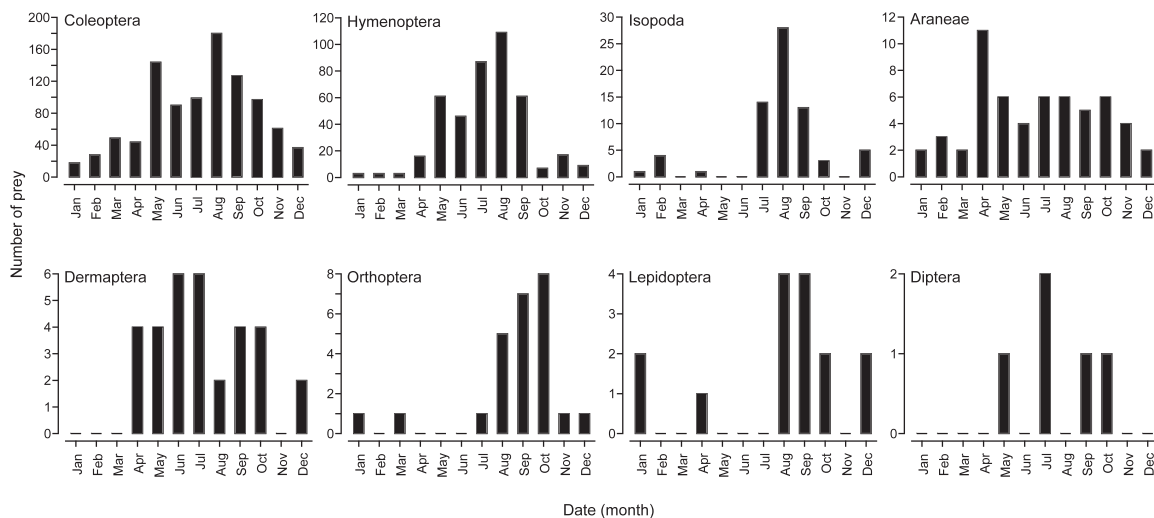


Figure 2.—Number of prey from eight different orders of arthropods consumed by *Latrodectus hesperus* spiders on a monthly basis in 2005. Taxa are presented in order of abundance (left-right).

polyphagous, and insects constitute the largest portion of their diets (Nentwig 1987); other common prey include arthropods such as spiders. However, particular prey taxa are often disproportionate represented in the diets of many polyphagous spider species (see species-specific diet breadth indices in Nyffeler 1999), as was found in this study.

Despite being polyphagous, *L. hesperus* showed a certain degree of dietary specialization on Coleoptera and Hymenoptera, and there was much variation in the prey composition of their diet across different months. It is not known whether this trend reflects habitat-related heterogeneity in prey availability. A study of *L. hesperus* populations in the San Juan Islands, located off the northwest coast of the USA 2 km from my study population, also found that spiders fed mostly on Coleoptera, especially tenebrionid, carabid and scarab beetles (Exline & Hatch 1934). Furthermore, previous research on the diets of other *Latrodectus* species across various habitats has also indicated that the prevalent prey type is Coleoptera. For example, in arid regions of Spain, *L. lilianae* (Melic 2000) feed on a variety of arthropod prey, although predominantly on Coleoptera, which make up the bulk of prey biomass (Hódar & Sánchez-Piñero 2002). Likewise, a foraging study of *L. geometricus* (Koch 1841) living indoors in Brazil revealed a predominance of Coleoptera in their diet among six orders of insects collected from their webs (Rossi & Godoy 2005). Dissections of nests from *L. revivensis* (Shulov 1948) and *L. tredecimguttatus* (Rossi 1790) in Israel and Palestine also showed a predominance of Coleoptera prey remains among several other types of arthropod prey (Shulov 1940, 1948; Shulov & Weissman 1959). Coleoptera are also disproportionately represented in the natural diets of species from other theridiid genera (Riechert & Cady 1983; Nyffeler & Benz 1988). However, *Latrodectus* spiders, including *L. hesperus*, are also important predators of Hymenoptera such as ants and wasps, as shown in this study. In fact, *L. hesperus* may exert a large influence on the activity patterns of ants (MacKay 1982). Examples of *Latrodectus* spiders that feed primarily on ants include *L. pallidus* (Pickard-Cambridge 1872) from Palestine and *L. mactans* (Fabricius 1775) living in cotton fields in Texas, USA (Shulov 1940; Nyffeler et al. 1988).

Conspecifics comprised a small fraction of the diet of *L. hesperus*, despite their facultative web-sharing habits at the study site (Salomon et al. 2010). Like most spiders, *L. hesperus* are opportunistic cannibals that only feed on conspecifics when hungry, when the availability of alternative prey types is low, or following an antagonistic encounter with a conspecific (Mayntz & Toft 2006; Wise 2006; M. Salomon & S. Vibert, unpublished data).

A spider's diet breadth may depend on several factors, including intrinsic factors such as prey-capture behaviour and foraging mode, extrinsic factors such as habitat characteristics and prey ecology, and combinations thereof (Riechert & Luczak 1982; Uetz 1990). Prey-capture behaviour may influence diet breadth in several ways. For example, theridiid spiders such as *L. hesperus* typically capture prey by 'combing' sticky silk around them with their back legs to immobilize the prey (Japyassú & Caires 2008). This foraging technique is thought to be particularly effective at capturing large or potentially harmful prey such as Coleoptera and Hymenoptera (Nentwig 1987). Furthermore, the range of prey sizes

captured may also depend on the extent of social interactions during foraging. Species in which individuals forage alone usually capture prey that are smaller or comparable in size, whereas social and partly-social spiders that cooperate during foraging can subdue large prey several times their size (Rypstra 1990; Powers & Avilés 2007). In this study, *L. hesperus* spiders fed on prey that were mostly 50–130% of their adult body size. Based on my many laboratory and field observations of foraging in *L. hesperus*, adults appear to capture and consume prey alone, even when they share webs, whereas juveniles often capture and consume prey as a group, especially large prey. The potent venom and effective prey-capture web of *Latrodectus* spiders may also contribute to the success of some individuals or species at capturing large prey (Forster 1995; Hódar & Sánchez-Piñero 2002). Furthermore, the distribution of prey sizes and taxa in the diet may depend on a spider's prey selectivity associated with particular dietary requirements. Spiders can discriminate between prey based on individual characteristics such as size, external morphology, behaviour and nutrient composition, and thus determine the prey's relative profitability (Riechert & Luczak 1982; Pekár 2004).

Likewise, a spider's foraging mode (i.e., web-based hunting versus cursorial hunting) may determine the ability to forage on a wide versus narrow range of prey types. In a meta-analysis of the diets of spiders living in agro-ecosystems, Nyffeler (1999) found that cursorial spiders generally have a larger diet breadth than web-building spiders. This difference is likely due to the lower accessibility of many prey types by stationary (web-based) versus mobile (cursorial) hunters, although it may concurrently depend on habitat characteristics (see below).

In web-building species, the morphology and location of the web may influence an individual's diet. Web morphology varies both across species and across individuals living in different environments, and a web's structural (e.g., overall geometry, silk thread density) and physical (e.g., position, orientation) characteristics may determine prey-capture rate and prey composition (e.g., Rypstra 1982; Sandoval 1994; Miyashita 1997). Furthermore, some of these web characteristics may represent adaptations for specialized feeding on profitable prey types, thereby narrowing the range of potential prey. For example, the prey-capture component of *L. hesperus* webs consists of sticky 'gumfooted' silk threads that function mostly as trip lines for ground-active arthropods such as Coleoptera and certain Hymenoptera (Blackledge et al. 2005).

Because prey are non-randomly distributed in space and time, the taxonomic composition of prey in a spider's diet largely depends on the location of its web within the habitat (Chacón & Eberhard 1980; Nentwig 1985; Harwood et al. 2001). A spider's actual diet may dependent on local prey diversity and seasonal activity patterns of prey, which determine feeding opportunities (Uetz 1990). By occupying a particular habitat location (either involuntarily or voluntarily) a web-building spider may have access to a specific subset of prey. At the study site in coastal British Columbia, *L. hesperus* spiders live exclusively under driftwood logs (Salomon et al. 2010), which likely restricts opportunities to feed on aerial prey or vegetation-borne prey, and constrains their diet breadth to ground-active arthropods.

The results of this study invite further research on the role of behaviour and life history in the feeding ecology of *L. hesperus*. For example, one could examine whether the diet of *L. hesperus* varies with age, which is likely correlated with prey-capture behaviour and dietary requirements. Based on field observations, I suspect that many of the ants collected as prey were preyed upon by *L. hesperus* juveniles and that subadult and adult females were the ones feeding on wasps. A relationship between predator age and feeding habits may provide insight into important aspects of a predator's biology, such as growth rate and reproductive success.

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Appendix 1.—List of regression equations used to calculate dry prey biomass (y , in mg) based on total body length (x , in mm) for different orders of arthropods. For Araneae prey, the calculations were based on tibia-patella length of leg pair I (tp , in mm) and wet prey biomass (w , in mg)

Prey taxon	Regression equation	R	R ²	Source
Coleoptera	$\ln(y) = -3.460 + 2.790 \ln(x)$	0.98	—	Rogers et al. 1977
Hymenoptera	$\ln(y) = -3.871 + 2.407 \ln(x)$	0.97	—	Rogers et al. 1977
Isopoda	$y = 0.010 x^{2.844}$	—	0.96	Hódar 1996
Dermaptera	$y = 0.002 x^{3.497}$	—	0.96	Hódar 1996
Orthoptera	$\ln(y) = -3.020 + 2.515 \ln(x)$	0.97	—	Rogers et al. 1977
Lepidoptera	$\ln(y) = -4.037 + 2.903 \ln(x)$	0.99	—	Rogers et al. 1977
Diptera	$\ln(y) = -3.293 + 2.366 \ln(x)$	0.96	—	Rogers et al. 1977
Araneae				This study
<i>Latrodectus hesperus</i> :	$\ln(w) = 1.948 + 2.032 \ln(tp)$ ($P < 0.0001$, $n = 86$)	—	0.23	
	$\ln(y) = -1.846 + 1.132 \ln(w)$ ($P < 0.0001$, $n = 32$)	—	0.92	
<i>Tegenaria agrestis</i> & <i>T. duellica</i> :	$\ln(w) = 3.038 + 1.253 \ln(tp)$ ($P = 0.007$, $n = 28$)	—	0.22	
	$\ln(y) = -1.745 + 1.100 \ln(w)$ ($P < 0.0001$, $n = 16$)	—	0.87	
Lycosidae:	$\ln(y) = -0.679 + 2.643 \ln(tp)$ ($P < 0.0001$, $n = 32$)	—	0.65	